

THE ONTOGENY OF THE THECIDACEAN BRACHIOPOD *MOORELLINA GRANULOSA* (MOORE) FROM THE MIDDLE JURASSIC OF ENGLAND

by P. G. BAKER

ABSTRACT. Investigation of fifty-five brachial valves and several sectioned shells from a new locality has led to the conclusion that in *Moorellina granulosa* the brachial apparatus shows progressive elaboration from simple tubercles to very delicate convoluted lobes which are in the form of a ptycholophe. Also that *Thecidium forbesi* Moore (1855) should be regarded as an early pre-brachial lobe stage of *M. granulosa*.

Five ontogenetic stages are described. The argument for an ontogenetic series is strengthened by the changes occurring in the cardinal process, coincident with the development of the brachial apparatus. Reference is made to the improbability of finding detached brachial valves showing adult characteristics. It is considered that the generic distinction between *Moorellina* Elliott (1953) and *Rioulina* Pajaud (1966) should be based on the form of the brachial lobes and not merely on their presence or absence. Specific determination based on the morphology of the brachial valve is considered unsatisfactory and a technique has been developed for the study of the internal characters of complete specimens.

THE paper records the occurrence of thecidellinids in the Oolite Marl of the Mid-Cotswolds. The deposit is rather variable and outcrops at a number of localities. It is well developed on Cleeve Cloud near Cheltenham where it attains a thickness of over 4 m. The Marl is typically a pale, cream-coloured marl, relatively harder and more oolitic in the upper layers, softer and with the ooliths more scattered towards the base. It thins in a north-easterly direction towards Chipping Campden and changes lithologically in a south-westerly direction, becoming indurated south from Painswick until it is indistinguishable from the overlying limestone.

Stratigraphically the Oolite Marl was placed by Arkell in the Lower Inferior Oolite (Upper Aalenian, *murchisonae* zone). It rests on a clearly recognizable bored surface of Lower Freestone but cannot be structurally separated from the overlying Upper Freestone, into which it passes laterally in the vicinity of Stroud.

The material described in this paper was obtained from the northernmost outcrop of the Oolite Marl two miles to the south of Chipping Campden at Westington Hill quarry, grid. ref. SP 142368. The Marl occurs at the top of the quarry which exposes almost 8 m. of Lower Freestone. The collection was made from a bed of soft, pale marl 30 cm. thick, which occurs in the north face of the quarry between two harder bands and about 60 cm. above the top of the Lower Freestone.

The thecidellinids from this locality occur together with a variety of organo-detrital remains which are recorded in tabular form in the text. This fauna is essentially similar to the surf-zone fauna recorded by Nekvasilová (1967) (Nekvasilová *in* Ager 1965, p. 146). The occasional large brachiopods which occur are forms which are anatomically characteristic (Ager 1965) of peri-reefal deposits.

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preparation of this paper. Thanks are due to Mr. M. Talbot, Geology Department, University of Bristol and Dr. L. R. M. Cocks, Department of Palaeontology, British Museum (Natural History) for the loan of Corallian and Inferior Oolite material for comparison purposes; to Mr. G. McTurk for preparing the stereoscan negatives; to Dr. G. F. Elliott for comments concerning certain morphological features; to Dr. A. W. Medd, Institute of Geological Sciences for identifying the polyzoa fragments and finally to Professor P. C. Sylvester-Bradley for use of the research facilities of the University of Leicester.

Registration of Material. The specimens figured and referred to in this paper are to be deposited in the museum collection of the Department of Geology, University of Leicester. The specimen numbers quoted refer to their catalogue numbers.

TABLE 1

Residue retained on sieve mesh						
Residue type	2mm. mesh		422 μ . mesh		152 μ . mesh	
	Av. ten 5gm.samps.	Av. % sample	Av. ten 5gm.samps.	Av. % sample	Av. ten 1gm.samps.	Av. % sample
Oolite fragments	3.8	4.7	40.8	0.78	—	—
Ooliths	—	—	1198.8	22.9	148.8	0.8
Brachiopod shell fragments	69.9	84.3	3555.0	68.0	17064.0	98.4
Bivalve shell fragments	3.8	4.7	45.0	0.84		
Echinoderm debris	1.8	2.2	214.8	4.1	64.5	0.3
Gastropods	—	—	0.3	0.006	—	—
Thecidellinids	0.2	0.24	14.4	0.27	2.6	0.01
Other brachiopods	1.4	1.6	13.8	0.26	5.7	0.03
Ostracods	—	—	8.4	0.16	38.9	0.2
Polyzoa fragments	1.7	2.0	112.2	2.1	2.0	0.01
Annelid worms	0.4	0.48	19.1	0.36	3.5	0.01
Total	83.0		5222.6		17330.0	

PREPARATION OF MATERIAL

Weathered marl samples were dried and crumbled through a 6-mm. sieve to remove large fragments. The sieved material was immersed in water and cleaned for ten minutes in a Dison electrosonic cleaner, marketed by Headland Engineering Developments Ltd. The samples were then washed until a clean residue was obtained. This was dried and passed through 2-mm., 422- μ , and 152- μ sieves, each residue size being analysed for faunal content (Table 1). Experience has shown that only the material retained on the 422- μ mesh is likely to yield thecidellinids. The cleaned residue was hand-picked under a binocular microscope and the brachiopods transferred to glass tubes for further cleaning. The individual tubes were replaced in the cleaner for periods of 10–20 seconds until the matrix had been removed. The shells were examined at each phase of cleaning

to determine whether the treatment should be continued. It should be emphasised that this is a very slow method of collecting as the thecidellinid content of the residue is approximately 0.3%. The collection of 172 specimens is comprised as follows:

Brachial valves	55
Pedicle valves	16
Complete specimens	43
Broken valves with significant detail	58
	172

Complete specimens selected for sectioning were cemented to glass slides, using a mixture of Lakeside cement (obtainable from Cutrock Engineering Co.) and chloroform. This remains plastic for sufficient length of time to allow correct orientation of the specimen under a binocular microscope. When the cement has hardened, the orientation of the specimen is checked and a plasticine mould is built round it. The mould is then filled with Ceemar cold setting resin, which, when hardened, allows the block (attached to the slide) to be serial sectioned on a Croft parallel grinder (see Hendry *et al.* (1963) for other methods). Although the theory of sectioning such small specimens at 0.02 mm. intervals is sound it is found to be inaccurate in practice. Better results are obtained if acetate peels are taken after a standard number of 30–50 revolutions (depending on the area of the block face). The length of the specimen is divided by the number of peels obtained, thus averaging out any error.

ANALYSIS OF RESIDUE

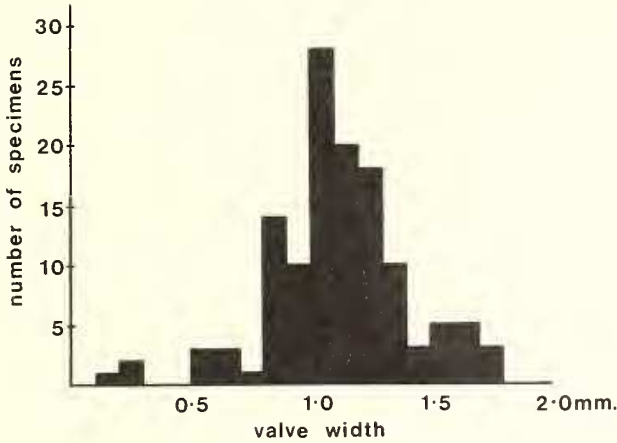
Residue obtained by the method described was found to constitute approximately 40% of the Oolite Marl from the Westington Locality. An analysis of the composition and faunal content of the cleaned residue is shown in Table 1.

In all size ranges, the bulk of the residue is composed of brachiopod shell fragments which may be identified as rhynchonellid and terebratuloid. Occasional specimens of *Globirhynchia subobsoleta* (Dav.), *Epithyris submaxillata* (Morris), and *Plectothyris fimbria* (Sow.) occur in the coarse residue and it is probable that the shell debris was formed from the remains of these species. The bivalve shell fragments may be identified as *Ostrea* and *Lopha* species. The echinoderm debris consists of unidentified echinoid spines and plates, crinoid ossicles of *Pentacrinus* type, unidentified ophiuroid plates and vertebrae. Three very small gastropods of *Nerinea* type were recovered from the 422- μ sample. The polyzoa fragments have been identified by Dr. A. W. Medd as *Actinopora* sp., *Berenecia* sp., *Meliceritites* sp., and *Spiropora* sp. The ostracods are *Bairdia* sp., *Cytherella* sp., and several unidentified cytheracean genera.

The analysis probably shows a bias towards brachiopod shell fragments as the true nature of the shell type was frequently obscured by adherent matrix. It is possible therefore, that some fragments included in the brachiopod count may in fact have been bivalve material. In addition, quite large echinoid spines appear in the 422- μ sample as their diameter is the critical factor. In the 152- μ size range it was not possible to distinguish between brachiopod and bivalve shell material with any degree of accuracy and

they are therefore grouped. However, as the proportion of brachiopod shell material is so large it is considered that the probable error is of no significance. Analysis of the brachiopod content was very critical and it is unlikely that any specimens escaped attention, even in the 152- μ samples. Although the number of ostracods shows a marked rise in this size range, they still represent approximately the same percentage of the sample.

The thecidellinid material shows the same ranges of variation of shell shape noted by Elliott (1948) during his study of *Bifolium* and by Nekvasilová (1967) during her study of *Thecidiopsis*. It appears to be correlated with the size of the area of attachment



TEXT-FIG. 1. Histogram to show the size distribution of 126 brachial valves of *Moorellina granulosa* (Moore) from Westington Hill Quarry. Number of individuals plotted against width of the brachial valve.

and is almost certainly the result of environmental influence (Rudwick 1962). The dangers of using a single character are evident but for the purpose of expressing size distribution (text-fig. 1) width of the brachial valve is used, as this appears to be one of the least variable growth characteristics. This feature is particularly useful as over half the material consists of complete or broken brachial valves.

Scars of the area of attachment on the pedicle valve occasionally show portions missing and occasionally, the pedicle valves are still cemented to shell fragments. Nekvasilová (1967) has shown that the form of the area of attachment is consistent with *Thecidiopsis* being attached, either to the valves of living oysters (liberated on the decay of conchiolin), or settled directly to some firm rocky substratum. The author is in agreement with her views on the ecology of *Thecidiopsis* and the evidence suggests that *Moorellina* occupied a similar environment, that is, belonged to the epifauna of the inner sub-littoral zone. This opinion is further supported by their association with peri-reefal brachiopods and the nature of the organo-detrital remains with which they are deposited (ref. Table 1).

A consideration of the evidence indicates that the collection represents a transported death assemblage, the size-frequency distribution (text-fig. 1), showing moderate positive skewness. This may be regarded as the product of a normal growth-mortality

rate if compared with the histograms plotted by Hallam (1967) in his work on molluscan death assemblages.

The fragmentation of thecidellinids, other brachiopods, bivalves, and Polyzoa indicates that the debris was formed in a turbulent environment. However, the lack of abrasion of the fragments together with the persistence of occasional bridges and brachial lobes in detached brachial valves of thecidellinids would suggest that the organo-detrital remains were transported only a short distance. Reference to Table 1 will show that thecidellinids are most common in the 422- μ size range whereas ostracods are most common in the 152- μ size range. Brachiopod shell fragments represent a high percentage of the material in all size ranges. These data and arguments advanced by Hallam (1967) suggest that no significant sorting of the population has occurred. The absence of appreciable numbers of small thecidellinids which would reflect the normally expected high juvenile mortality rate may simply be the result of selective shell breakage (Hallam 1967, p. 35). The presence of brachiopod shell fragments in excess of 2 mm. diameter, the absence of large thecidellinids and particularly the absence of large thecidellinid shell fragments, is considered to indicate that thecidellinids with a brachial valve width of more than 2 mm. are not represented in the population. Sedimentation factors are not thought to have affected the upper size limit as oolites larger than the largest complete thecidellinid shells are common in the 422- μ sample. Clearly, therefore, the larger size-distributions of the sample may be regarded as adult shells. This is a much smaller population than that studied by Nekvasilová (1967) but the ratio of brachial valves to pedicle valves and complete shells within the sample is similar.

The material shows a number of progressive changes, such as, the development of the cardinal process, the development of the border and the appearance and progressive elaboration of the sub-peripheral rim. The brachial apparatus develops in the same manner and, in the tuberculate stages, forms with from one to five pairs of brachial tubercles are present. For reasons to be described later it is thought that some of these latter are damaged adults. All the structures, with the exception of the adult brachial lobes, show varying degrees of development in the material studied. This shows the presence of an intimate relationship between the progressive development of the various growth features with general size increase.

The collection of the material from one sample from a single bed, the size distribution and the close parallel between the growth stages of *Moorellina* and the ontogenetic development of *Bifolium* (Elliott 1948), *Lacazella* (*B.*) *laczelliforme* (Elliott) (Nekvasilová 1964), and *Thecidiopsis* (Nekvasilová 1967) leaves little room for doubt that the material from Westington Hill quarry represents the ontogenetic stages of a single species.

Comparison of the forms having a single pair of brachial tubercles with *Thecidium forbesi* Moore 1855 indicates that there is no valid basis for the separation of *T. forbesi* from *Moorellina granulosa*. It is proposed, therefore, that the adolescent growth stages showing this degree of development of the brachial apparatus should be designated forbesiform. It is considered that five ontogenetic stages may be recognized, each marked by the appearance of a characteristic feature (text-fig. 3A-F). The dimensions recorded are those of the specimens figured in Plate 73 and are intended to indicate only the general size relationship, the stages represented being obviously subject to natural size variation.

	<i>Length mm.</i>	<i>Width mm.</i>	<i>Thickness mm.</i>
A. Brephic valve	0.47	0.5	0.2
Pre-forbesiform stage	0.9	1.0	0.3
C. Early forbesiform stage	1.0	1.2	0.35
D. Late forbesiform stage	1.2	1.6	0.35
E. Post-forbesiform stage	1.4	1.7	0.4
F. Adult valve	1.1	1.3	0.4

MORPHOLOGY

The present paper is concerned only with the morphology of the interior of the brachial valve (text-fig. 2A) but it is felt that some attempt should be made to reconcile the interpretations of Elliott (1948) and Pajaud (1963) with the glossary laid out in the *Treatise on Brachiopoda* but without adding to the existing confusion. Briefly the new morphological terms and the justification for their introduction are as follows:

Border. The term is introduced to define the flat region of the valve between the sub-peripheral rim and the periphery of the valve. This unites the limbe-marginal and bord frontal of Pajaud and enables the distinction between anterior, lateral, and postero-lateral regions to be made. It is felt that this is necessary as it is noted that the postero-lateral border is the first to appear during the pre-forbesiform stage of development (text-fig. 3B).

Brachial shelf. The term is introduced to define the raised flat areas, within the lophophorian area, from which the brachial tubercles develop. The inner boundary of the shelf is occasionally raised to form low ridges which may correspond, in part, to the ridge extensions described by Elliott (1948) during the early ontogeny of *Bifolium faringdonense* (Davidson).

Brachial tubercle. The dotted brachial ridge (Elliott) is not thought to be sufficiently explicit. The rounded dots (Elliott 1948, p. 9) are by definition tubercles (Williams 1965, H154) and the term brachial tubercle is introduced as these structures are of considerable importance in the development of the brachial apparatus.

Socket ridges. As defined in the glossary, inner and outer socket ridges are present (Pl. 74, fig. 3).

The recommendation of the glossary (op. cit. H148) that the term marginal flange should be replaced by sub-peripheral rim is adopted but it is noted that this has a postero-lateral extension demarcating the outer boundary of the cardinal area. The term brachial lobe introduced by Pajaud (1966b) for the establishment of the genus *Rioltina* is adopted, particularly as lobes are referred to in Moore's original description of *Moorellina granulosa* (Moore 1855). One must recognise however, that the brachial lobes of *M. granulosa* are convoluted and not as in *Rioltina*, auriform.

Ontogenetic stages recognized. The brephic valve (text-fig. 3A; Pl. 73, fig. 1) is the first stage represented and is 0.5 mm. wide. The valve is almost circular, thick, and cap-like. The cardinal margin is almost straight and approximately two-thirds of the width of the valve. The cardinal process is the only recognizable thecidellinid feature, being low

and broad, occupying a little more than half the hinge-line and projecting slightly beyond the cardinal margin (text-fig. 2B). There is no median septum but the postero-lateral border is just discernible. The dental sockets are poorly developed but clearly bounded anteriorly by the lateral divergence of the sides of the cardinal process, forming inner socket ridges where they turn down to unite with the posterior margin of the valve. No sub-peripheral rim is present at this stage. Three valves show this stage of development.

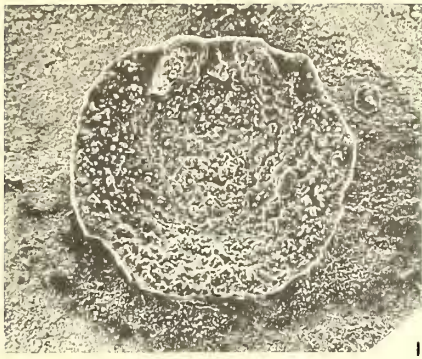
Stage two is marked by the appearance of the median septum which is considered to be a neanic feature (text-fig. 3B; Pl. 73, fig. 2). The valve is still nearly circular, relatively thick, markedly convex, and in the specimen figured, 1 mm. wide. The cardinal margin is slightly curved and somewhat less than half the width of the valve. The cardinal process is more strongly developed (text-fig. 2C) and turns down sharply into the floor of the valve anteriorly. The postero-lateral border is now clearly defined, also the dental sockets. The sub-peripheral rim is represented by a row of denticles which, posteriorly, mark the inner boundary of the postero-lateral border, not, as in Elliott (1948), trending inwards to form the sides of the cardinal process. Laterally the denticulate rim is almost peripheral so that there is no noticeable border. It will be noticed that the bridge extensions do not unite with the inner socket ridges and that they merge laterally with the sub-peripheral rim. The median septum is fairly thick, developing from the anterior margin and extending posteriorly, the posterior portion being free from the floor of the valve. This stage is designated pre-forbesiform by virtue of the fact that the brachial tubercles of *T. forbesi* Moore (1855) are not yet developed. Six valves show this stage of development.

The two stages described correspond closely with the first two ontogenetic stages of *Bifolium faringdonense* (Davidson) described by Elliott (1948) but the subsequent stages showing the development of the brachial apparatus are quite different.

Stage three is marked by the appearance of the brachial tubercles characteristic of *T. forbesi* and is accordingly designated the forbesiform stage, early and late features being distinguishable (text-fig. 3C, D; Pl. 73, figs. 3, 4). The valve is now slightly wider than long. The cardinal margin is well-defined, slightly curved, and just less than half the width of the valve. The cardinal process is by now a prominent feature, projecting markedly beyond the cardinal margin. The dental sockets are deep and the postero-lateral border inclined to the plane of the valve. The sub-peripheral rim is well developed so that the lateral and anterior portions of the border are now visible. At this stage the

EXPLANATION OF PLATE 73

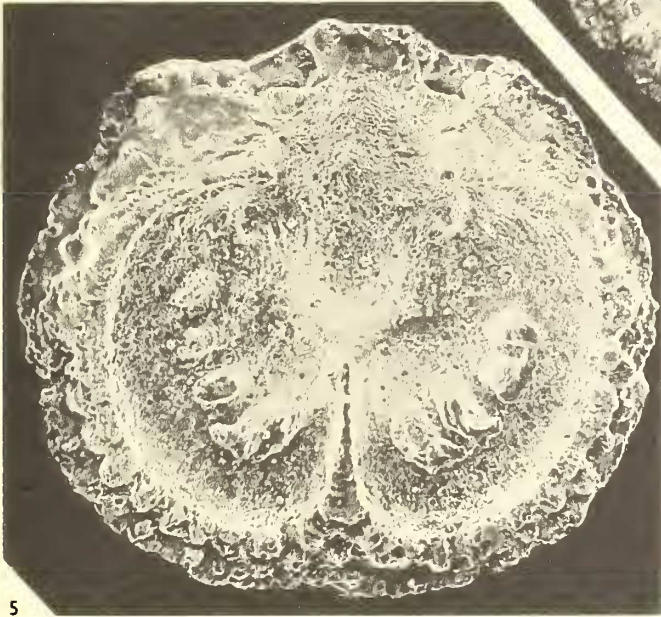
Figs. 1-6. Stereoscan photomicrographs of brachial valves of *Moorellina granulosa* (Moore) collected from the Oolite Marl, Westington Hill Quarry near Chipping Campden. All the figures are interior views of specimens coated with evaporated aluminium before photography. The bridge is broken on specimens fig. 3-5. 1. Brephic valve (37500), shell recrystallized. $\times 75$. 2. Pre-forbesiform stage of development (37503) showing the development of the median septum. Cardinal process slightly damaged. $\times 50$. 3. Early forbesiform stage (37505) showing the brachial shelf and appearance of the first pair of brachial tubercles. $\times 50$. 4. Late forbesiform stage (37507) showing four pairs of brachial tubercles, well defined sub-peripheral rim and border. $\times 50$. 5. Post-forbesiform stage (37508) showing the expanded brachial tubercles, uniting posteriorly to form arches. Cardinal process slightly damaged. $\times 50$. 6. Adult valve (37509) showing the form of the right brachial lobe. Cardinal process slightly damaged. $\times 50$.



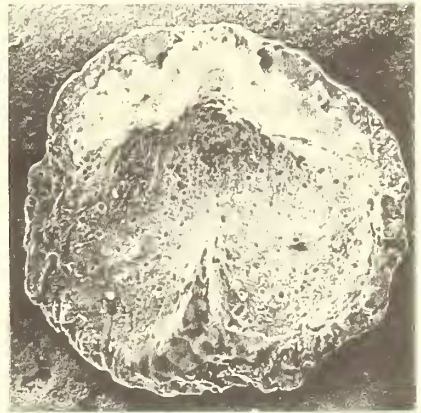
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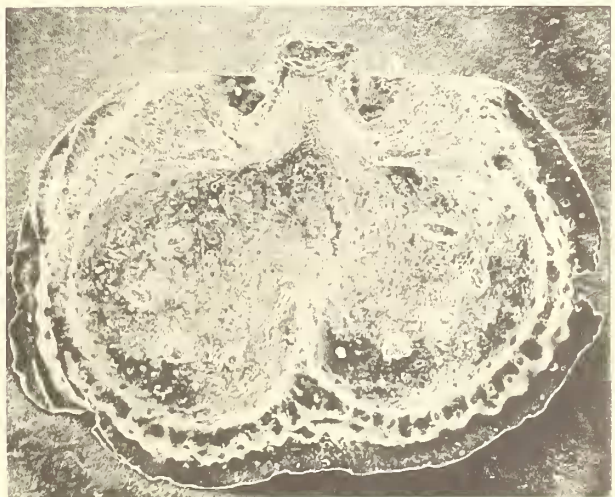
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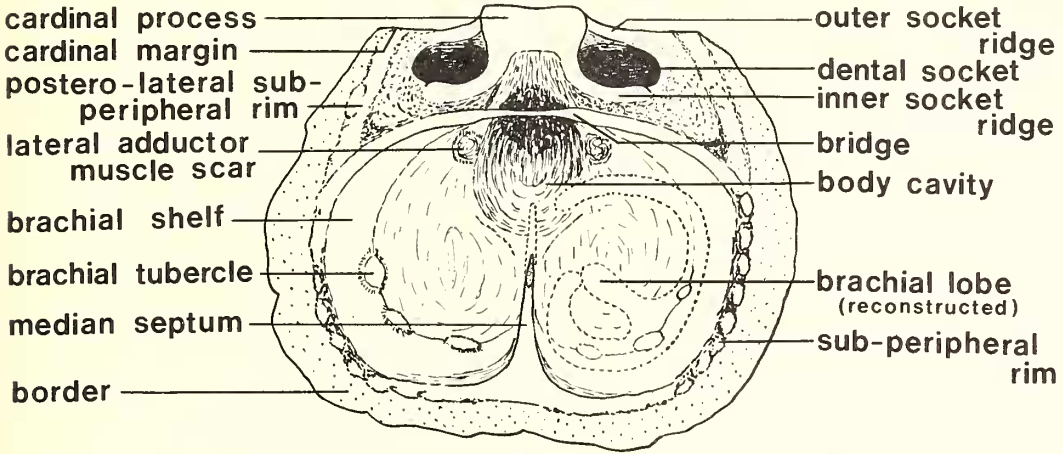


3



4

bridge is usually complete (broken in the specimen figured during cleaning) but without the marsupial notch (Elliott 1948). The posterior portion of the median septum is quite clearly free from the floor of the valve and is usually slightly larger than that shown. The floor of the valve is now characterized by two raised areas (brachial shelf), along



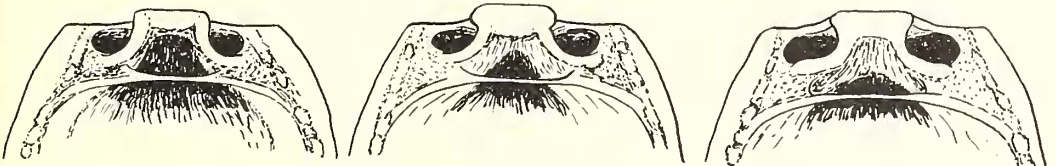
A



B

C

D



E

F

G

TEXT-FIG. 2. A. Composite drawing from brachial valves 37509 and 37510 to show the morphological features of the interior of the adult valve. Brachial lobe and median septum reconstructed from specimen 37510. B-G. Drawings to show the form and modification of the cardinal process during ontogeny, together with the development of the inner and outer socket ridges. B, brephic 37500. C, preforbesiform 37503. D, E, early forbesiform 37505, 37506. F, late forbesiform 37507. G, post forbesiform 37508.

the inner boundary of which the brachial tubercles develop, usually appearing in pairs. Valves with one or two pairs of tubercles are said to constitute an early forbesiform stage, whilst those with four to five pairs are said to constitute a late forbesiform stage. Attention is drawn to the fact that the tubercles are regularly arranged and without the random distribution figured by Pajaud (1966*b*) in his work on material from the

Inferior Oolite of Dundry. During the early forbesiform stage the cardinal process begins to lose its concavity posteriorly (text-fig. 2D, E) eventually forming a flattened region which gives rise to the outer socket ridges during the late forbesiform stage (text-fig. 2F; Pl. 74, fig. 3). The bulk of the valves show this stage of development.

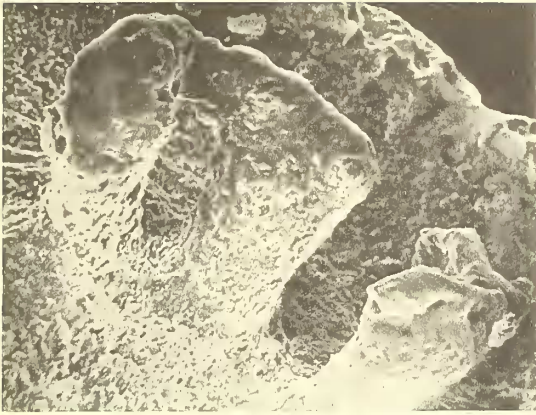
The beginning of stage four may be recognized by the fact that the distal ends of the brachial tubercles expand and develop projections which ultimately unite with those of adjacent tubercles to form delicate arches. This degree of organisation is taken to represent a post-forbesiform stage (text-fig. 3E; Pl. 74, fig. 1) The cardinal margin is, by definition, a hinge line. The outer socket ridges, developed from the posterior of the cardinal process are now clearly visible (text-fig. 2G; Pl. 73, fig. 5). The median septum extends back almost as far as the edge of the body cavity. The floor of the valve is characterized by expanded brachial tubercles showing the development of arches and inward pointing projections. The brachial shelf is now hardly visible, its decline probably to be correlated with the higher development of the brachial apparatus. Five valves show this stage of development.

In the adult state, stage five, the arches of the post-forbesiform stage are united, thickened, and extended to form convoluted lobes (text-fig. 3F). Two specimens were found at this stage of development, 37509 with the right brachial lobe intact (Pl. 73, fig. 6; Pl. 74, fig. 2) and 37510 with the left brachial lobe intact. The brachial lobes of both specimens could be seen to be joined to brachial tubercles anteriorly. An attempt to clean specimen 37510 in order to provide conclusive evidence for the view that the brachial lobes are attached to the valve solely by brachial tubercles, resulted in the loss of the remaining brachial lobe. Specimen 37509 has therefore been subjected only to partial cleaning, this in itself being sufficiently destructive to remove part of the bridge. This specimen is remarkable in possessing a very young form cemented to its anterior border in front of the median septum (Pl. 74, fig. 4).

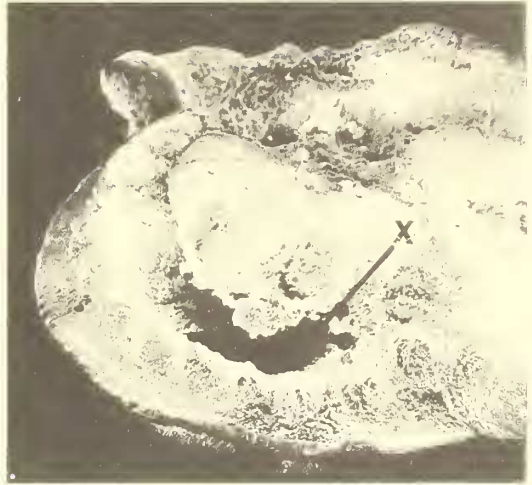
For reasons to be mentioned later, very little appears to be known about the adult brachial valve of *M. granulosa*. The above specimens are almost certainly examples of the type referred to by Davidson (1874, p. 110) in Moore's collection from Dundry and almost identical with Moore's type specimens, M2850, Nos. 2, 5, and 6 held in the basement of the City of Bath Reference Library. The Westington Hill specimens are smaller than the examples of *M. granulosa* held at the British Museum. These have a brachial valve width of 2.5–3.5 mm. whereas the largest specimens from Westington Hill have a

EXPLANATION OF PLATE 74

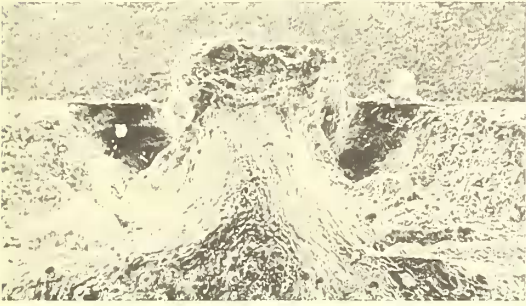
Figs. 1–8. *Moorellina granulosa* (Moore) 1. Stereoscan photomicrograph (37508) showing the brachial arches. Postero-lateral view, angle of incidence 48° to the plane of the valve. $\times 250$. 2. Stereoscan photomicrograph (37509) showing the brachial lobe free from the floor of the valve. X indicates the point of attachment to one brachial tubercle. Antero-lateral view, angle of incidence 36° to the plane of the valve. $\times 100$. 3. Stereoscan photomicrograph (37507) normal to the plane of the valve showing the cardinal process with inner and outer socket ridges. $\times 100$. 4. Very young form cemented to the anterior border of specimen 37509. $\times 250$. 5. Photomicrograph, reflected light. Vertical transverse section through specimen (37511) showing the posterior extensions of the brachial lobes and median septum. $\times 46$. 6. Retouched copy of fig. 5. 7, 8. Photomicrographs prepared from acetate peels of vertical transverse sections of specimen (37511) at 0.68 and 0.7 mm. from the umbo, showing the form of the brachial lobes and their attachment to the floor of the valve by brachial tubercles. $\times 50$.



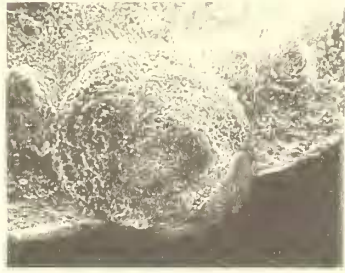
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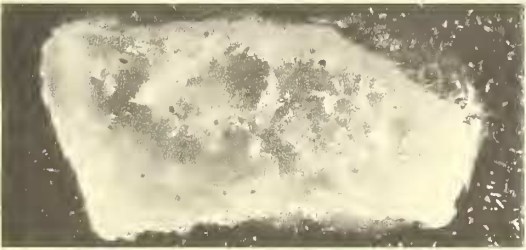
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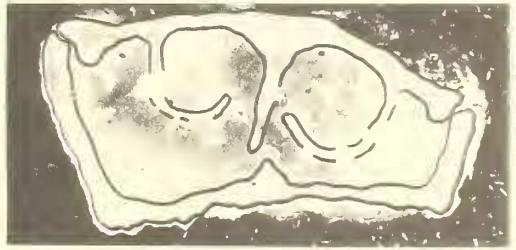
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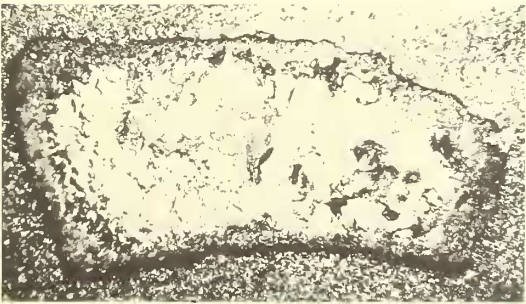
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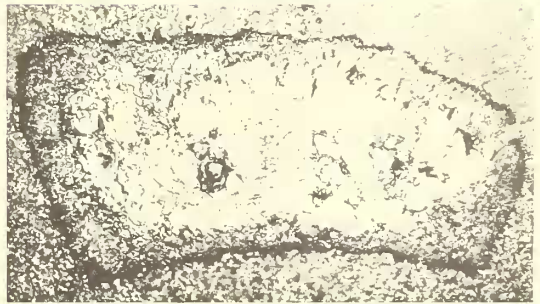
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6



7



8